Effects of Vegetation Patches on Soil Nutrient Pools and Fluxes within a Mixed-Conifer Forest

Heather E. Erickson, Patricia Soto, Dale W. Johnson, Brent Roath, and Carolyn Hunsaker

Abstract: At a spatially heterogeneous mixed-conifer forest in the central California Sierras, we quantified total carbon (C) and nitrogen (N), inorganic N, and net N mineralization in organic (O) and surface (0–15 cm) mineral soils, and in situ fluxes of inorganic N and ortho-phosphate using resin lysimeters under three patch types: closed canopy conifer, sparsely vegetated open canopy, and *Ceanothus cordulatus* thickets. In O horizons, total N and C pools ranked: closed canopy > *Ceanothus* > open canopy. In mineral soils, total N pools under *Ceanothus* exceeded those under closed canopy patches by about 30%. For 2 years, nitrate concentrations and rates of net N mineralization in O horizons were 4× greater under *Ceanothus* than under the other patch types. Similarly, ammonium concentrations and net N mineralization in mineral horizons were more than 80 and 200% greater, respectively, under *Ceanothus* than under the other patch types. In situ fluxes of nitrate were 4× greater beneath *Ceanothus* for 1 year, and no differences were found among the patch types for another year. Despite the interannual variability, our data suggest that *Ceanothus* contributes to a greater proportion of total N mineralized than based on cover alone, and may be important for forest nutrition under current conditions and after forest burning. FOR. SCI. 51(3):211–220.

Key Words: Soil nitrogen, soil carbon, net nitrogen mineralization, *Ceanothus*, Sierra Nevada forests, *Abies concolor*.

FOR OVER A CENTURY, many coniferous forests in the western United States were subject to fire suppression. These forests are now being considered for thinning and burning as a means to remove accumulated fuels and restore the structural conditions that characterized the forests before suppression (North et al. 2002). How a forest responds to these treatments may depend, in part, on the soil conditions that result from the treatments. For example, while forest burning may increase available pools of nitrogen (N) (Neary et al. 1999), total N pools may decrease (Caldwell et al. 2002, Smith et al. 2000) with potentially negative consequences for forest productivity over the long term (e.g., Monleon et al. 1997). However, these responses are not consistent across all forests (Wan et al. 2001). Moreover, N availability has been shown to affect seedling performance in eastern mixed temperate forests (Catovsky and Bazzaz 2002) and western cedar-hemlock forests (Bennett et al. 2003), and has the potential to alter successional dynamics (Catovsky et al. 2002). Thus, having a better understanding of how burning and thinning affects N cycling and dynamics would greatly improve our ability to predict future conditions.

How a forest responds to thinning and burning may also depend on soil conditions before disturbance. Available and total pools of N and carbon (C) stores are inherently variable in forest soils (Homann et al. 2001, Conant et al. 2003, Rothe et al. 2002). Within-stand variation in nutrient cycling and soil properties has been attributed to tree species composition (Zinke 1962, Boerner and Koslowsky 1989, Finzi et al. 1998, Venterea et al. 2003), tree mortality pockets (Matson and Boone 1984), and physiographic features (Venterea et al. 2003). Whether pretreatment soil variability remains following forest conversion or restorative treatments is not well known, largely because the causes of the spatial variation in forest soils are still poorly understood.

Mixed-conifer forests range throughout the western United States, including much of California. Structurally, these forests exhibit a striking degree of spatial heterogeneity. In addition to a mixture of several species of conifers (hence the name), many mixed-conifer forests also contain areas of substantially reduced canopy cover, either completely without woody vegetation or containing thickets of shrubs. Although open canopy areas often have shallow soil depths to bedrock, many have soil depths capable of supporting permanent tree cover.

Heather E. Erickson, School of Science and Technology, Universidad Metropolitana, PO Box 21150, San Juan, Puerto Rico 00928-1150—ericksonheather@yahoo.com. Current address: 12410 SE McGillivray Boulevard, Vancouver, WA 98683. Patricia Soto, School of Science and Technology, Universidad Metropolitana, PO Box 21150, San Juan, Puerto Rico 00928-1150. Dale W. Johnson, Department of Environmental and Resource Science, University of Nevada, Reno, NV 89557—dwj@cabnr.unr.edu. Brent Roath, USFS, Sierra National Forest, Clovis, CA 93611. Carolyn Hunsaker, USFS, Pacific Southwest Research Station, Fresno, CA 93710.

Despite the prominent aboveground heterogeneity within mixed-conifer forests, few studies have documented how belowground resources vary among patches. Exceptions exist for some woody shrubs, which are capable of symbiotically fixing N_2. In the eastern Sierra Nevada, Johnson (1995) found that soils under *Ceanothus velutinus* contained more total C and N than soils under adjacent patches of Jeffrey pine. Oakley et al. (2003) found greater inorganic and total N in the litter layers under *Ceanothus cordulatus* than under another shrub, *Arctostaphylos patula.* This suggests that N-fixing associated shrubs, such as *Ceanothus* sp., may be important in retaining or rebuilding N stocks after restoration. Documenting heterogeneity of soil resources at the patch scale is not only crucial for understanding how a forest might respond to restoration or other management treatments, but also for accurately scaling estimates of soil C and N storage to landscape and regional scales.

In this study we sought to examine the relation between vegetation patch types and soil nutrient pools and processes at a mixed-conifer forest located within the Teakettle Experimental Forest in central California. The forest consists of distinct patches of conifers (primarily white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), and sugar pine (*Pinus lambertian*)), low-stature shrubs (*C. cordulatus* and *A. patula*), and sparsely vegetated open areas, all located on a nearly consistent southern-facing slope. We hypothesized that areas with low vegetative cover would contain lower pools of C and N, lower inorganic N concentrations, and lower fluxes of N and phosphorus (P) in contrast to areas with dense forest vegetation and shrub cover. We also expected that soils under *C. cordulatus* would have greater N availability and greater stores of total C and N than the other patches. To test these hypotheses, we conducted intensive studies for more than 2 years across replicated patches of the three major patch types at Teakettle: closed canopy mixed-conifer, *C. cordulatus* thickets ("*Ceanothus*"), and open canopy areas lacking significant vegetation and without exposed rock.

Methods
The Teakettle Experimental Forest

The Teakettle Experimental Forest (36°58′N, 119°2′W) is a 1,300-ha old-growth forest reserve (mean elevation = 2,200 m) located on the western slope of the central Sierra Nevada Mountains in California. The climate is Mediterranean with warm dry summers and cool winters. Most of the 1,000-mm annual precipitation falls as snow. The mixed-conifer forest at Teakettle is spatially heterogeneous with a discontinuous canopy consisting of primarily conifer-dominated tree patches containing combinations of white fir (*Abies concolor* [Gordon and Glend.] Lindley), incense cedar (*Calocedrus decurrens* [Torrey] Florin), red fir (*Abies magnifica* A. Murr), sugar pine (*Pinus lambertiana* Dougl.), or Jeffrey pine (*Pinus jeffreyi* Grev. and Balf); shrub patches consisting of primarily mountain whitethorn (*Ceanothus cordulatus* Kellogg), chinquapin (*Chrysolepis sempevirens* [Kell.] Hjelmq.), or greenleaf manzanita (*Arctostaphylos*

patula E. Greene); and open canopy areas lacking permanent woody vegetation (North et al. 2002). Open canopy patches can have a diverse, but sparse (~0.2%, North et al. 2005) herbaceous cover (e.g., mountain pennyroyal [*Monardella odoratissima* Benth.], lupine [*Lupinus adsurgens* E. Drew], and scarlet gilia [*Ipomopsis congesta* {Hook.} V. Grant]), and often contain allochthonous litter from adjacent conifer patches.

Soils in the study area are mostly well-drained Xerochrepts, Xerumbrepts (Inceptisols), and Xeropsamments (Entisols) formed from decomposed granite. Textures range from gravelly coarse sandy loams to gravelly loamy coarse sands of the Cannell and Cagwin series, respectively. Although several lightening strikes have occurred in recent decades within Teakettle, the last major fire to occur in the area was 1943, but no impact was made on the study areas (North et al. 2002).

As detailed in North et al. (2002), in 1998 a series of 18 4-ha plots were established at Teakettle to assess the effects of burning and thinning as tools for restoration. The 4-ha size was chosen to sufficiently capture the spatial variability inherent in vegetation in the mixed-conifer forest at Teakettle (North et al. 2002), in that all of the patch types are included in each of the plots. The plots range in elevation from about 1,950 to 2,270 m. The aspect is southerly with slope angles ranging from 5 to 20°. The 18 plots fall into one of six treatments as part of the restoration experiment. We used eight of these plots to locate replicate patches (see below) for the current study, which was completed before the restoration experiment began; thus the results we present describe pretreatment conditions.

Patch Description and Selection

The three dominant patch types, closed canopy, open canopy, and *Ceanothus*, occur throughout Teakettle. Canopy cover ranges from 79% in closed canopy patches to 32% in open canopy patches (North et al. 2002; note—canopy cover was measured with a moose horn which, because of a 30° view angle from vertical, incorporates foliage from adjacent patches). Although sizes and densities of the patches vary within and among the patch types (for example, patch sizes may range from 3 m² for *Ceanothus* to 1,000 m² for conifer tree groups), each 4-ha plot contained a sufficient number of each of the patch types for replicated sampling. For this study, a potential patch needed to have consistent vegetation for at least 10 m in any one direction and cover a minimum area of 40 m². Ongoing research at Teakettle suggests that some of these patches may have originated as recently as the 1970s, perhaps linked to drier climatic conditions that occurred during that time (Dave Rizzo, personal communication, University of California, Davis, March 2004). Furthermore, there is little evidence to suggest that the patches have changed since that time. Based on a cluster analysis of vegetation data obtained from 402 regularly spaced grid points covering a 72-ha area within Teakettle, North et al. (2002) estimate that closed canopy conifer represents 68% of the area, shrub thickets

13%, open canopy 11%, and the remainder composed largely of exposed rock. *Ceanothus* represents 75% of the shrubby area (North et al. 2005).

Fifty-four patches, three replicates of the three dominant patch types (closed canopy, open canopy, and *Ceanothus*) within each of six of the 4-ha plots were selected in 1999. In 2000, six additional patches of each type from two additional plots were sampled for a total of 72 patches (3 patch types × 3 replicate patches × 8 plots).

Soil Sampling and Analyses

In 1999, organic (Oi and Oe) and surface mineral horizon soils (0–15 cm) were collected from the 54 patches and used to determine inorganic nitrogen (N), net N mineralization using aerobic laboratory incubations, total pools of carbon (C) and N, pH, and bulk density. In 2000, soils were collected from 18 new patches as well as from 18 of the patches previously sampled. Due to time limitations, not all patches could be sampled in 2000.

Within each patch, a measuring tape was centered along the longest axis to select three evenly spaced sampling points that were at least 3 m from the edge of a patch. At each point, O (10 × 10 cm, sampled to depth) and surface mineral horizon (2 cm diameter corer, 0–15 cm) soils were collected and pooled by patch. Depths of the O horizon were recorded to the nearest 0.5 cm; if depths less than 1 cm were encountered no sample was taken. Soils were collected July 6–8 in 1999 and July 7 in 2000, kept cold in coolers and brought to the USFS PSW Laboratory in Fresno, CA within a few days for processing.

Organic horizon soils were sieved (5 mm) to remove coarser litter particles and large roots. Mineral soils were also sieved (2 mm) to remove roots, dead buried wood, and coarse mineral fractions. For extractable inorganic N pools, sieved soils (5 and 10 g for O and mineral horizons, respectively) were extracted with 100 ml 2 M KCl by shaking for 30 min, then stored overnight. The extract was filtered (0.45 μm), stored frozen, and sent to the USDA International Institute of Tropical Forestry (IITF) in Rio Piedras, Puerto Rico for automated colorimetric analysis (Alpkem, Wilsonville, OR) of NO_3^- and NH_4^+. To estimate net N mineralization, we used 10-day aerobic incubations at constant moisture and temperature (25°C); hence differences in N mineralization should be primarily due to differences in substrate quality or factors not related to soil moisture. Because soil moisture was often already low by early July in both O (ranging from 6.5 to 42.8% for open and closed canopy, respectively) and mineral horizons (ranging from 6.4 to 9.8% for open and closed canopy, respectively), to avoid moisture limitations (Stanford and Epstein 1974) incubating samples were wetted to about 55% water holding capacity (38% and 12% gravimetric moisture contents for O and A horizons, respectively). Net N mineralization was calculated as the change in $NH_4^+ + NO_3^-$ over the 10 days and net nitrification as the change in NO_3^-. Additional subsamples were dried for gravimetric moisture contents (70°C for 48 hours) and ground with a mortar and pestle for

total C and N analyses by dry combustion on a LECO-CN analyzer (LECO Corporation, St. Joseph, MI) at IITF or Universidad Metropolitana. Soil pH was measured on 5- and 25-g field moist subsamples, using soil:distilled water ratios of 1:5 and 1:1, for organic and mineral samples, respectively.

Bulk density was measured in July 1999 or 2000, depending on plot. For the O horizon, a precisely measured 15 × 15 cm square hole was dug adjacent to the center sampling point in each patch, and carefully excavated of organic material. Wood greater than 1 cm diameter was discarded. Depths were recorded from several points on each side to calculate volume. For the A horizon, a 5 cm-diameter soil corer was used to remove soil from two depths, 0–7 cm and 7–14 cm, from a single location also adjacent to the center sampling point. Mineral soils were sieved to remove fractions >2 mm; coarse fractions were weighed and converted to volume using a rock density of 2.16 g/cm^3, obtained by measuring masses and volumes by water displacement on five 70-g coarse fraction samples. For the mass estimates, organic and mineral soils were dried for 48 h at 70°C and 101°C, respectively, before weighing. Volumes of the coarse fractions were subtracted from core volumes to calculate mineral horizon bulk densities, and the averages of the two depths were used for subsequent calculations. Soil depths and rock content adjusted bulk densities were used to calculate total pools of C and N and net N mineralization on an area basis (Boone et al. 1999). Rock fractions are expressed on a mass basis.

Inorganic N and P Fluxes

Soil solution fluxes were measured with resin lysimeter collectors (Susfalk and Johnson 2002). In the autumn of 1999 and 2000, two lysimeters containing anion-cation exchange resins were inserted into the soil in two-thirds (i.e., 54) of the patches where N mineralization was measured. The resin lysimeters consisted of a 5.5-cm long, 4-cm inside-diameter (12.57 cm^2 area) PVC pipe within which 10 g of oven-dried Rexyn I-300 (H-OH) resin were trapped between two Nitex nylon sheets. Each end of the lysimeter outside of the resin section was filled with a 20 g layer of moist, washed silica sand. To keep the sand in the tube until installation, the bottom of each PVC tube was covered with cheesecloth held in place with a rubber band. The resin collectors were removed and replaced annually. The resins were extracted with 2 M KCl and analyzed for NH_4-N, NO_3-N, and ortho-P by automated colorimetric analysis by the Water Analysis Laboratory at the Desert Research Institute in Reno, NV. Fluxes were calculated from the amount of nutrient in the resin minus blanks divided by the surface area of the resin lysimeter.

Statistical Analyses

Differences among patch type and year for most variables were analyzed using a randomized block design with replication using General Linear Models (SAS Institute,
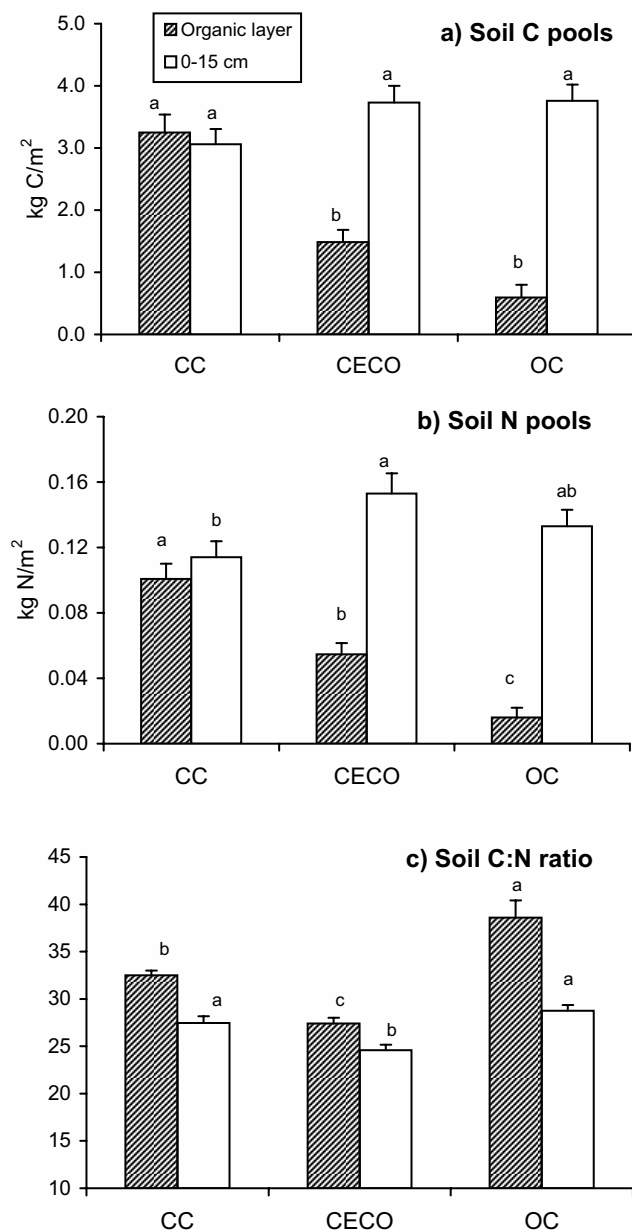
Figure 1. Total carbon (a), nitrogen (b), and C:N ratios (c) for O and surface (0-15 cm) mineral horizons for the three patch types. Codes for patch types are listed in Table 1. Different letters indicate significantly different means by patch type and within a horizon. Error bars indicate 1 SE, *n* = 24.

Inc.). The effect of patch was tested as Mean Square (MS) Patch/MS Patch∗Plot, with the interaction term treated as a random effect (Underwood 1997). For data collected over 2 years, the effect of year was examined using data from patches that were sampled in both years. If year was significant, separate analyses were done by year using all of the data for that year. If year was nonsignificant, data were pooled by patch across years before testing for the effect of patch. The effect of year was not examined for total pools, pH, or bulk density. In most cases, the effect of plot, treated as a block in the model, was not significant (data not presented). A Tukey's multiple comparisons test was used to indicate significant differences for means across patch types. Typically, data were log-transformed to stabilize variances. We also explored possible relationships between rates of N cycling (e.g., net N mineralization and nitrification) and various soil properties. Parametric correlation analyses were used after verifying that model assumptions were not seriously violated.

Results

Nutrient Pools and Dynamics in Patches

Closed canopy organic (O) horizons were less acidic by half a pH unit compared with the O horizons in the other two patch types (Table 1). Mineral soil pH varied by only 0.2 pH units among the patch types (Table 1), with soils under open canopy slightly more acidic than the others. Bulk density of the O horizons was highly variable and there were no differences among the patch types (Table 1). However, in surface mineral horizons bulk density was almost 20% greater in open canopy patches than in *Ceanothus* or closed canopy patches. Open canopy mineral soils also contained a greater proportion of rock fractions than soils in closed canopy patches (Table 1).

Total pools of C and N in the O horizons, excluding those in woody debris, differed significantly among patch types and ranked closed canopy > *Ceanothus* > open canopy ($P < 0.001$, Figure 1) and corresponded with the ranking of the mass of O horizon (Table 1). Total C pools in the O horizon under closed canopy were two times greater than C pools in *Ceanothus* patches and, not surprisingly, over five times greater than O horizon C pools in open areas (Figure 1). Similarly, total N pools in the O

Table 1. Selected characteristics of organic (O) and 0-15-cm mineral soils (mean, 1 standard error (SE)) for the three dominant patch types at the Teakettle Experiment Forest.

Patch type	O horizon mass (kg/m²)	Depth of the O horizon (cm)	Soil pH (H₂O)		Bulk density (g/cm³)		Rock fraction (% of mass)
			O horizon	0-15 cm	O horizon	0-15 cm	0-15 cm
OC	1.1 (0.4)[c]*	1.0 (0.3)[c]	5.0 (0.15)[b]	5.7 (0.06)[b]	0.101 (0.02)[a]	1.12 (0.03)[a]	22.6 (1.54)[a]
CECO	3.3 (0.4)[b]	3.0 (0.4)[b]	5.1 (0.08)[b]	5.9 (0.09)[a]	0.121 (0.01)[a]	0.91 (0.03)[b]	19.5 (1.25)[ab]
CC	6.8 (0.6)[a]	5.5 (0.4)[a]	5.5 (0.9)[a]	5.9 (0.06)[a]	0.124 (0.01)[a]	0.95 (0.03)[b]	16.2 (1.30)[b]

Codes for patch type are: OC, open canopy areas; CECO, *Ceanothus cordulatus*; CC, closed canopy conifer. For O mass, O depth, mineral horizon bulk density, and rock fraction, *n* = 24. For O horizon bulk density, *n* = 24 except for OC, where *n* = 13 (see text). For pH, *n* = 18 except for OC O horizon, where *n* = 13.
* Different superscripts within columns indicate significant effects ($P < 0.05$) using Tukey's multiple comparison.
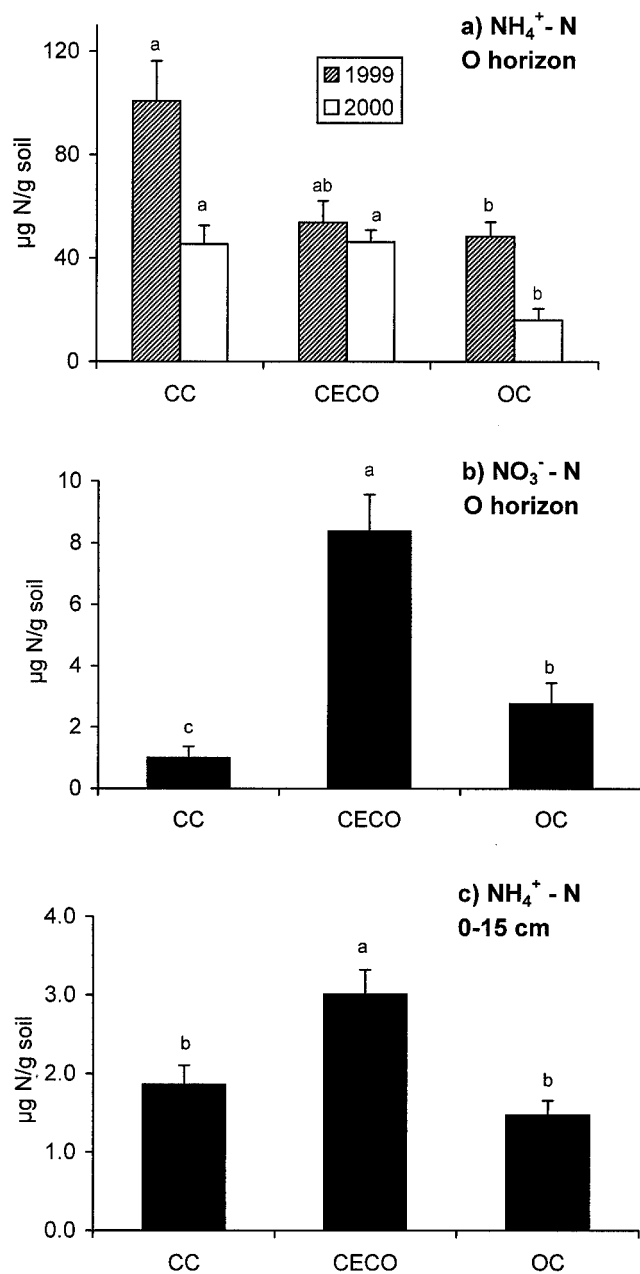
Figure 2. Extractable NH_4^+ (a) and NO_3^- (b) for O horizon soils and extractable NH_4^+ (c) for surface mineral horizon by patch type. For all variables, the effect of patch type was significant. Where results are shown for 2 years, the effect of year was also significant. Different letters indicate significantly different means by patch type or by patch type within year if data are for 2 years. Error bars indicate 1 SE. Where results are presented for 2 years, $n = 18$ and 14 for 1999 and 2000, respectively; otherwise, $n = 24$. For O horizons under OC, $n = 8$ and 6 for 1999 and 2000, respectively.

horizon under closed canopy exceeded those under *Ceanothus* and open areas. Across all patches ($n = 71$), O horizon depth was highly correlated with O horizon total C (Pearson's $r = 0.900$, $P < 0.0001$) and N pools (Pearson's $r = 0.817$, $P < 0.0,001$). Total C pools in the upper 0–15-cm mineral horizons (mean = 3.5 kg/m^2) did not differ among the three patch types ($P = 0.063$) (Figure 1); however, patch type did have a significant effect on N pools in this horizon ($P = 0.019$). Here, total N pools under
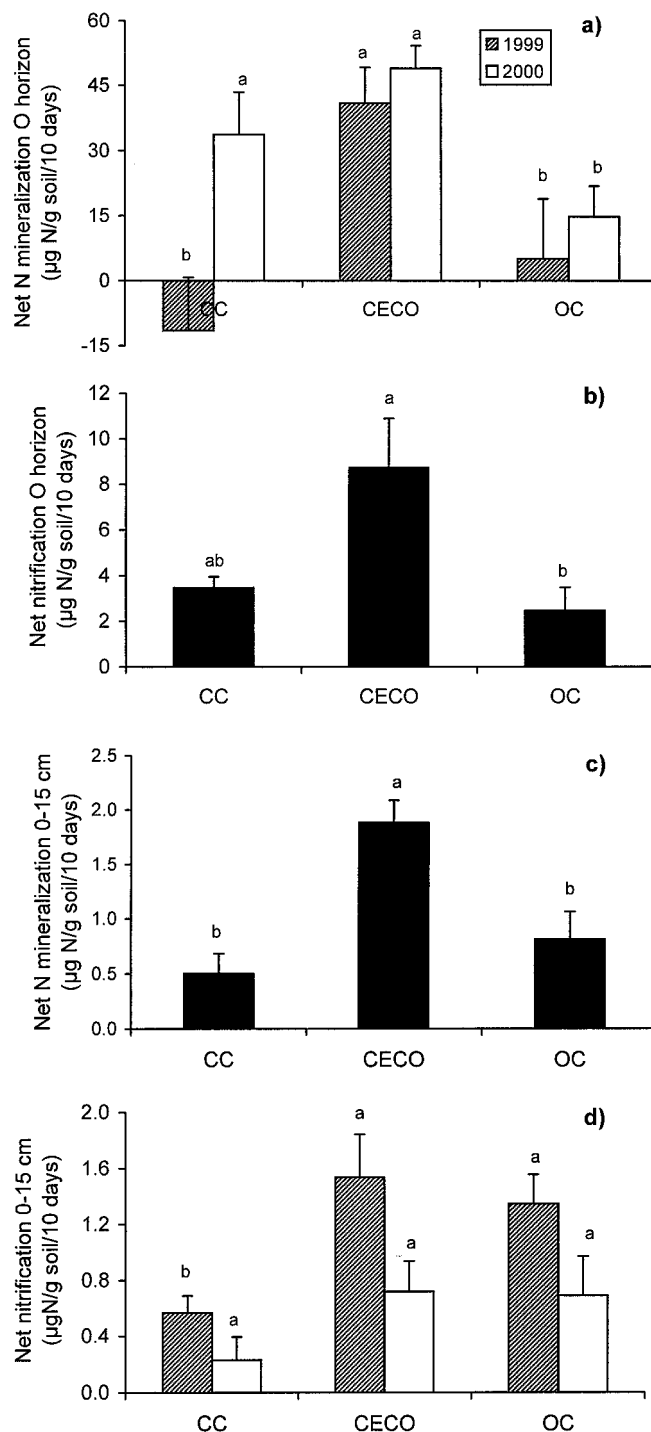

Figure 3. Net N mineralization, and net nitrification for O horizon (a, b) and upper (0-15 cm) mineral (c, d) soils by patch type, respectively. For all variables, the effect of patch type was significant. Where results are shown for 2 years, the effect of year was significant. Different letters indicate significantly different means by patch type or by patch type within year if data are for 2 years. Error bars indicate 1 SE, sample sizes are explained in Figure 2.

Ceanothus significantly exceeded those under closed canopy by about 34% (Figure 1). Carbon:nitrogen ratios for both O and upper mineral horizons were significantly lower under *Ceanothus* than under closed canopy or open canopy (Figure 1).

Inorganic N, often considered an instantaneous measure

Table 2. Net N mineralization and net nitrification expressed on an area basis (mg N/m^2 of patch for 10 days) (mean, SE) pooled over 2 years for the three dominant patch types. Codes for patch types are defined in Table 1, $n = 24$.

Patch type	O horizon		0-15 cm	
	Net N mineralization	Net nitrification	Net N mineralization	Net nitrification
OC	27.8 (27.5)[a]*	3.3 (1.5)[b]	135 (29.2)[b]	182 (32.9)[a]
CECO	142 (30.3)[a]	23.4 (5.5)[a]	261 (38.4)[a]	176 (4.5)[a]
CC	133 (84.9)[a]	23.4 (3.1)[a]	86.8 (32.1)[b]	64 (16.8)[b]

* Different superscripts within columns indicate significantly different rates ($P < 0.05$) using Tukey's multiple comparison.

of N availability, differed among patch types and for extractable NH_4^+ in O horizons, also depended on year. In 1999, extractable NH_4^+ in O horizons was twice as high under closed canopy as under the other two patch types, while in 2000, extractable NH_4^+ was equally high under *Ceanothus* and closed canopy (Figure 2). Extractable NO_3^- was nearly an order of magnitude less than extractable NH_4^+ and was consistently higher under *Ceanothus* than under closed canopy or open canopy (Figure 2). Ammonium pools (Figure 2) in the upper mineral horizon were significantly greater in *Ceanothus* patches than in the other patch types. Nitrate was not detected in mineral soils (detection limit = 0.8 μg/g) under closed canopy and was only occasionally present under open canopy and *Ceanothus*, and was highly variable (data not shown).

Differences among patches were apparent for N dynamics, and often depended on year. In 1999, O horizons under closed canopy showed net immobilization rather than net mineralization (mass basis, Figure 3), whereas in 2000 net N mineralization was positive under closed canopy and did not differ significantly from net N mineralization in *Ceanothus* patches. On average, rates of net nitrification in the O horizon ranged from 19 to 31% of net N mineralization. Net nitrification in the O horizon was not influenced by year ($P > 0.05$), but as with the other variables, was influenced by patch type; net nitrification was greater under *Ceanothus* compared to the others (Figure 3). Rates of net nitrification on a mass basis in mineral horizons were much lower than rates in O horizons and differences among patches also depended on year; in 1999 nitrification in closed canopy was 40% less than in the other patch types, and in 2000 there were no significant differences among patch types (Figure 3). Rates of net N mineralization in the upper mineral horizon were nearly three times greater in *Ceanothus* patches compared with the other patch types (Figure 3).

Converting rates of N mineralization to an area basis

shows the importance of the mineral horizon in contributing to N turnover for all patch types (Table 2). Whereas net N mineralization expressed on a mass basis is roughly an order of magnitude less for mineral horizons than for O horizons (Figure 3), on an area basis rates in the mineral horizon are similar to or greater than those in the O horizon (Table 2). Similar to results expressed on a mass basis, net N mineralization on an area basis in surface mineral horizons for *Ceanothus* patches were more than two times greater than for closed and open canopy patches.

Nutrient fluxes were measured in 2000 and 2001. In 2000, nitrate, ammonium, and ortho-phosphate fluxes were highly variable and there was no effect of patch type (Table 3). In 2001, only nitrate fluxes differed significantly among the patches; here, nitrate was more than four times greater in *Ceanothus* than the other patch types (Table 3). Nutrient fluxes were much greater in 2000 than in 2001 (Table 3). No correlations were found between nutrient fluxes and KCl-extractable N or rates of net N mineralization ($P \gg 0.05$).

Discussion

Differences among Patches

Soil properties and belowground nitrogen dynamics appear to reflect the highly heterogeneous aboveground ecosystem of the mixed-conifer forest at Teakettle. The three dominant patch types, closed canopy, *Ceanothus*, and open canopy, had distinct signatures for a number of soil properties and N cycling processes. For example, extractable nitrate in the O horizon, a variable showing large differences among patch types, was 8.5 and 3.0 times greater in *Ceanothus* versus closed and open canopy patches, respectively. Similarly, net N mineralization in the upper mineral soil was 3.8 and 2.3 times greater in *Ceanothus* versus closed and open canopy patches, respectively. Ma et al. (2004) also found large differences in soil respiration rates among patch types; here, rates were 90 and

Table 3. Inorganic N and P fluxes (kg/ha) (mean, SE) as measured by resin lysimeters in surface soils of the three dominant patch types.

Year	Patch Type	NO$_3$-N	NH$_4$-N	PO$_4$-P
2000	OC	1.76 (1.49)[a]*	0.64 (0.35)[a]	0.41 (0.16)[a]
	CECO	2.42 (1.08)[a]	1.64 (0.84)[a]	1.95 (1.25)[a]
	CC	2.45 (1.22)[a]	1.71 (0.71)[a]	0.68 (0.24)[a]
2001	OC	0.19 (0.04)[b]	0.48 (0.07)[a]	0.07 (0.02)[a]
	CECO	2.21 (1.43)[a]	1.28 (0.53)[a]	0.42 (0.21)[a]
	CC	0.24 (0.07)[b]	0.68 (0.09)[a]	0.13 (0.04)[a]

For 2000, $n = 12$ patches per type; for 2001, $n = 8$ patches per type. Codes for patch types are defined in Table 1.
* Different superscripts indicate significantly different fluxes ($P < 0.05$) within a given year using Tukey's multiple comparison.

165% higher in closed canopy areas and *Ceanothus* patches, respectively, than in open canopy areas.

In general, the effect of species composition on within-stand soil properties has been examined in more detail than effects of aboveground patches on soil properties. For example, in a closed canopy eastern temperate forest, C and N pools and net N mineralization differed under various tree species (Finzi et al. 1998). Similarly, Boerner and Koslowsky (1989) found tree species explained much of the variation in N mineralization and C concentrations in an eastern mixed species forest. Zinke (1962) first reported differences in soil N concentrations among several California conifer species. Though tree species and site were often confounded in this classic study, the findings suggest that some of the variation found within the closed canopy patches at Teakettle may be due to variations in species composition. For example, N concentrations were 20% greater under incense cedar than under *P. ponderosa* (Zinke 1962). More research is necessary at Teakettle and in mixed-conifer in general to assess tree species level effects on soil properties. Furthermore, forest pathogens, which may also change rates of net N mineralization (c.f. Matson and Boone 1984), are another potential source of variation in the N cycle within the closed canopy patches at Teakettle. As documented in North et al. (2002) several root disease/bark beetle/dwarf mistletoe complexes are found in Teakettle. While recognizing the importance of these and other factors in potentially contributing to the variation in soil properties within the closed canopy patches at Teakettle, we found that the greatest amount of variation for most soil properties was between, not within, the different patch types.

Low or negative rates of net N mineralization are expected in most coniferous forest soils (Davidson et al. 1992, Hart et al. 1994), as well as low concentrations of and short-term net turnover of NO_3^-. The dominant patch type, closed canopy, was consistent with this expectation in that N mineralization in the O horizon was negative one year and NO_3^- concentrations were low (O horizon) or not detectable (mineral horizon). In many conifer forests in the Sierra Nevada, water availability is thought to limit tree distributions and net primary production (Miller and Urban 1999), although it is likely that semi-arid ecosystems are also co-limited by nitrogen (Hooper and Johnson 1999, Powers and Reynolds 1999). Sierran forest soils often show high microbial N immobilization (Johnson et al. 2000, Davidson et al. 1992) and have thick forest floors (Johnson et al. 2000). That relative rates of nitrification were low across all patch types in this study supports the idea of low N availability and N limited processes in mixed conifer forests.

Ceanothus patches have the largest total N pools in surface mineral soils, lowest soil C:N ratios, highest rates of net N mineralization, net nitrification and NO_3-N concentrations in the O horizon, and the highest rates of net N mineralization and NH_4-N concentrations in the mineral horizon. Johnson (1995) also found greater rates of N mineralization under *C. velutinus* in contrast to under adjacent

pines at an eastern Sierra site. Presumably, many of these differences are due to symbiotic N fixation by *Ceanothus*. While several studies have estimated in situ N fixation rates for *C. velutinus* (e.g., Busse 2000), a common shrub in northern California and southern Oregon, we know of no work quantifying fixation rates for *C. cordulatus*. Results from a pilot study using the del ^{15}N natural abundance method of estimating symbiotic N_2 fixation suggest that *C. cordulatus* obtains a significant (but unknown) portion of its annual N requirement from fixation (Erickson 2000). The increased total N under *Ceanothus* relative to the conifer patches is consistent with other studies showing greater soil N pools under N-fixing trees and shrubs (c.f. Binkley and Sollins 1990, Johnson 1995). Perhaps as Johnson (1995) proposed, stabilization of organic matter might also play a role in maintaining high pools of C and N under *Ceanothus*.

Taken together, our results suggest that *C. cordulatus* makes a significant contribution to the N economy of the mixed-conifer forests at Teakettle. The sums of net N mineralization for the O and upper mineral horizons (Table 2) for *Ceanothus* and closed canopy patches are 403 mg N/m^2 and 220 mg N/m^2 per area of patch type, respectively. Multiplying these rates by the proportion of the forest area covered by each patch type (10 and 68% for *Ceanothus* and closed canopy, respectively), we calculate a forestwide contribution to net N mineralization of 40 mg/m^2 for *Ceanothus* and 149.6 mg/m^2 for closed canopy. Thus *Ceanothus*, although covering only 10% of the forest area, potentially contributes to over 25% of the N mineralized in the forest. (Note: This estimate is based on laboratory incubations only and assumes field rates would follow a similar pattern.) Whether neighboring conifers are able to use the additional N is largely unknown. Although conifer regeneration is relatively low in *Ceanothus* patches (H. Erickson, personal observation), fruiting bodies of ectomycorrhizal fungi have been found in *Ceanothus* patches (M. North, personal communication, June 2003), suggesting that the ectomycorrhizal conifers may be benefiting from a lateral transfer of nutrients.

N may cycle faster under *Ceanothus*, in part because of the greater N often found in litter produced by N fixers. Fresh leaf litter from *C. cordulatus* at Teakettle contains 1.27% N and has a mean C:N ratio of 42, in contrast to needle litter from the major *Abies* and *Pinus* sp. at Teakettle, with average N concentrations and C:N ratios of 0.62% and 82, respectively (H. Erickson, unpublished data). Litter C:N (or lignin:nitrogen) ratios have been shown to relate inversely to rates of net nitrogen mineralization in surface soils for a number of temperate (Pastor et al. 1984, Scott and Binkley 1997) and tropical forest ecosystems (Erickson et al. 2001). We also found inverse relationships for soil C:N ratios and rates of net nitrogen mineralization in O (Pearson's $r = -0.349$, $P = 0.007$, $n = 59$) and mineral horizons (Pearson's $r = -0.352$, $P = 0.002$, $n = 72$), suggesting that soil organic matter quality, expressed as the C:N ratio, also affects the rate of N mineralization.

Open canopy areas are mostly devoid of vegetation, but have thin (average 1.0 cm) accumulations of allochthonous

litter from adjacent patches. The high C:N ratios of these O horizons suggest low rates of decomposition: the litter layer appears relatively undecomposed and fibric and sapric layers are lacking. These high C:N ratios are also consistent with the low rates of net N mineralization. In mineral soils, the intermediate rates of N cycling and intermediate N pools sizes found under open canopies likely reflect, in part, plant species compositions within the patches. Several *Lupinus* sp. are also found growing in open areas. Many lupines are known to symbiotically fix N and could be adding a significant but unknown contribution to the N pools in open areas. Also, higher concentrations of nitrate in open versus closed canopy areas may reflect reduced plant uptake in those patches.

Allochthonous litter (i.e., from conifers) also falls into *Ceanothus* patches (H. Erickson, personal observation), presumably modifying soil properties in those patches resulting solely from input of *Ceanothus* litter. Nonetheless, O horizons are shallower under *Ceanothus* patches compared with closed canopy. This difference could be due to either greater litter input or slower decomposition in the closed canopy patches compared to the *Ceanothus* patches, or a combination of the two processes. Based on C:N ratios alone, *Ceanothus* litter would be expected to decompose more rapidly than conifer needle litter.

Obviously litter inputs, allochthonous or otherwise, are not as large in open patches as in the patches with woody vegetation, but apparently what gets there remains. Decomposition is influenced by litter quality and by environmental factors. We measured extremely low July soil moisture contents in open canopy areas (averaging 6.4% for mineral horizons over 2 years). Ma et al. (2004) report the highest soil temperatures at 10 cm depth (mean 20.0°C) for open canopy areas at Teakettle. Cooler soil temperatures and higher moisture contents within *Ceanothus* and closed canopy patches are more conducive to decay than the low moisture and high temperatures of open areas which likely limit microbial activity and rates of decomposition, at least during extended droughty periods. Mack and D'Antonio (2003) experimentally showed a strong microclimate control of net N mineralization during the dry season in a Hawaiian woodland. The Hawaiian soils in the dry season were three times moister than the open canopy soils at Teakettle, suggesting a strong potential for soil moisture limitation of soil processes within the patches at Teakettle. Collectively, our data suggest that the major differences in soil properties among the patch types at Teakettle are due to a combination of the quantity and quality of organic matter inputs and the steep differences in microclimate reported by Ma et al. (2004).

Year-to-Year Variations

Inorganic N pools are often highly variable within and among years, especially in highly seasonal ecosystems (St. John and Rundel 1976, Cain et al. 1999). Inorganic N may accumulate during periods of little rainfall (St. John and Rundel 1976, Davidson et al. 1992, Jensen et al. 2001). We attempted to collect soils within a few weeks after snowmelt; the lack of any difference in soil moisture between years ($P > 0.05$; data not shown) suggests that the differences we found in ammonium concentrations between years were not driven by differences in soil moisture. We also found large differences in net N mineralization within closed canopy patches; one year showed net N immobilization and the other year net N release. While sampling soils in 1999, an unusual early July rainfall moistened the dry forest floor and may have stimulated microbial immobilization (Pulleman and Tietema 1999). However, because the soils were incubated at 55% water holding capacity, other factors (e.g., microbial populations, substrate availability) likely influenced the shifting pattern of immobilization and release between the two years.

The smaller soil fluxes of inorganic N and P for the second year may have been due to differences in the amount of soil water flux, concentrations in soil water, or both. Total rainfall was nearly 30% lower the second year, but unfortunately, the resin data alone do not allow us to differentiate between the two factors.

The year-to-year variation in ammonium availability, net N mineralization, and nutrient fluxes results in year-to-year variation in patch effects as well. For example, in 2001 nitrate flux was significantly greater in *Ceanothus* patches compared to the other two patch types, but not in 2000 (Table 3). This underscores the importance of multiyear sampling for determining how dynamic variables differ among the different patches.

Implication for Restoration

Our key finding of significant differences among patch types for pools of C and N and rates of N transformations has an important implication for restoration. Burning, with or without forest thinning, is likely to become a key restoration tool in the Sierra Nevada. Because much of the burning-related losses of C and N from forests in the Sierra are due to combustion of the O horizon (Caldwell et al. 2002), legacies may remain in pockets of mineral soils that could affect future regeneration and survival. The different vertical distributions of C and N among the patch types suggest that their losses would be greatest in closed canopy patches, where a larger amount of total C and N pools is stored in the O horizon (Figure 1). And, because a larger proportion (nearly 50%) of total pools from the organic and mineral horizons is stored in aboveground litter in closed canopy patches, if a fire consumed most of the organic horizons, *Ceanothus* and open canopy areas would retain more of their original pools than the conifer patches.

Assuming mineral pools remained unchanged with consumption of the O horizon, there would no longer be any differences among the patch types for pools of C. However, the large amount of N stored in surface mineral horizons under *Ceanothus* suggests that even with intense burns, belowground patches of high N may remain under former *Ceanothus* patches. We also found lower C:N ratios in soils under *Ceanothus*; the inverse correlation between soil C:N

ratio and net N mineralization suggests that rates of N turnover would also be faster under former *Ceanothus* patches. For example, Oakley et al. (2003) found that inorganic N pools were greater under *Ceanothus* 6 months after burning compared with adjacent *A. patula* patches. These high N patches may be important if natural regeneration is N limited (c.f. Fransen et al. 2001). Furthermore, because N immobilization may increase after fire on N limited sites (Bell and Binkley 1989), such as within the conifer patches, the differences in N availability between the high N former *Ceanothus* patches and the likely N limited conifer patches may widen.

Our findings strongly suggest that *Ceanothus* patches and perhaps open canopy areas, which tended to have greater mineral horizon N pools than closed canopy areas, may be important for future forest regeneration and productivity. However, other potentially competing processes could diminish this effect. For example, open canopy soils, with greater rock fragment volumes and higher bulk density than the other soils, may not retain sufficient moisture for seedling establishment after fire. Also, resprouting of *Ceanothus* is often common and rapid after fire, suggesting that *Ceanothus* may again dominate N-rich sites after disturbance. Ongoing studies at Teakettle are monitoring the response of *Ceanothus* and conifer seedling establishment to burning and thinning treatments.

The characteristics of the N cycle that we measured for the conifer patches at Teakettle, however typical of mixed-conifer forest, may reflect the history of fire suppression. White fir, a shade-tolerant conifer, has increased in abundance in many mixed-conifer forests in the region because of the lack of natural fires (e.g., Stephenson 1999). Within the conifer patches at Teakettle, white-fir regeneration is abundant (North et al. 2002) presumably also due to lack of fire. However, because we did not examine how shifts in conifer species composition may have altered N cycling, we have no way of knowing whether the current patterns within the closed canopy patches are an artifact of fire suppression.

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